Pacific Science (1975), Vol. 29, No. 1, p. 31-50
Printed in Great Britain

Distribution and Ecology of the Marine Toad, *Bufo marinus*, in Papua New Guinea[1]

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ABSTRACT: *Bufo marinus* was introduced into the New Guinea region in the late 1930s. Its present distribution in Papua New Guinea is mapped. In the Port Moresby area, the population of *Bufo marinus* is capable of reproduction at any time of the year. Sampling at a rain forest and a savanna site near Port Moresby showed that the density of savanna toads is 10 times that of rain forest toads but that the rain forest toads are longer and heavier. This size difference probably results from the greater amounts of food and a larger proportion of proteinaceous food in the stomachs of rain forest toads. No native frogs appear to have been displaced by the successful invasion of the toad. Similarly, no native animals have become apparent toad predators. The literature on *Bufo marinus* ecology is summarized.

THE PROPENSITY of the marine toad (*Bufo marinus*) for insects and savannas has caused man to introduce this species into many South Pacific islands. The toad was primarily introduced to control insects associated with sugarcane and has been fairly successful in reducing insect damage to this crop (Wolcott 1937). While reducing the frequency of insect pests, the toads have multiplied and have themselves reached pest proportions in many areas. This superabundance is apparent in the urban and human-exploited areas of Papua New Guinea and has provided us with the opportunity to study their ecology.

Through our present investigation, we proposed to document the toad's current distribution in order to follow accurately its expansion or contraction of range. We also wished to obtain basic ecological data on toads in Papua New Guinea. With these data we can deduce the factors permitting successful invasion and the possibility of native faunal displacement.

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DISTRIBUTION

Following the early success of *Bufo marinus* as a biological control agent on Oahu, the Hawaiian Sugar Planters' Association actively distributed this toad throughout the other Hawaiian Islands and made it available to their Pacific neighbors (Oliver 1949). The initial introduction into Papua New Guinea at Keravat, East New Britain, occurred in February 1937 (Commonwealth of Australia 1938: 79-80) and the toads are purported to have been received directly from the Hawaiian Islands. The toads were introduced to control the sweet potato moth, *Hippetion celerio*, which was a serious pest in New Guinea at that time. Apparently, some measure of success was achieved as the 1939 Report to the League of Nations (Commonwealth of Australia 1940: 80) says that, "The Giant Toad, *Bufo marinus*, is being distributed to various parts of the Territory to control this pest." Because the territories of New Guinea and Papua were administered separately prior to World War II, this report implies that the introductions were limited to the Territory of New Guinea.

We have been unable to document accurately the date or place of the first introduction of the toad on the main island of New Guinea. Hearsay evidence relates an attempt to use the toads for human pregnancy tests at the Port Moresby Hospital in 1938, and, when they were found to

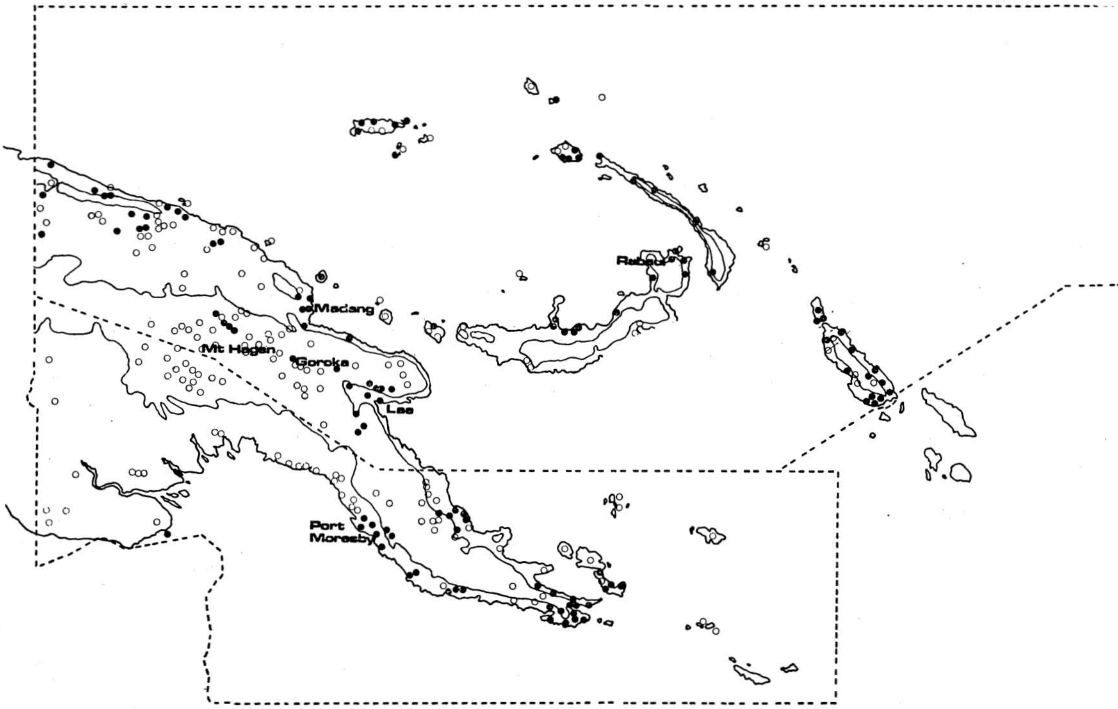

FIGURE 1. Distribution of *Bufo marinus* in Papua New Guinea in 1972. Solid circle, presence of toad; open circle, absence; thin line, 300-m contour.

be unsatisfactory, they were either released or escaped.

The distribution of *B. marinus* as of 1972 is mapped in Figure 1. Both the toad's presence and absence from a locality (see also Appendix 1 for detailed district list) have been plotted to provide a documented base for future studies of the dispersal of the toad. These data were obtained by sending a circular to all agricultural field staff, all local government councils, and all schools in Papua New Guinea. Apart from very few records, all localities for *B. marinus* are below or adjacent to the 300-m contour. The major areas of occurrence are centered around towns such as Lae, Port Moresby, or Rabaul. Population densities are high in urban areas and rapidly decrease as the habitats become less disturbed. *B. marinus* also inhabits primary lowland rain forest, for single individuals have been seen in the rain forest near Port Moresby, Garu village on West New Britain, and Madang. This pattern of abundance in Papua New Guinea seems to be the same as that within toad's natural range in Central and South America, although there have been no ecological studies of the marine toad to document the observations. Our current knowledge of marine toad biology has been obtained predominantly from introduced populations. Because of this, we lack the necessary base for the comparison of our data.

ANALYSIS OF ECOLOGICAL DATA

Materials and Methods

To estimate the possible effect of *Bufo marinus* on the native New Guinean frogs, we collected data on reproduction, food habits, and relative abundance. Two sampling localities were selected in the Port Moresby area (Figure 2): (1) a eucalyptus savanna habitat was represented by a site at the Moitaka sewage plant and associated road, approximately 14 km north of Port Moresby; (2) a rain forest habitat was represented by a section of the Brown River Road approximately 24 to 34 km north of Port

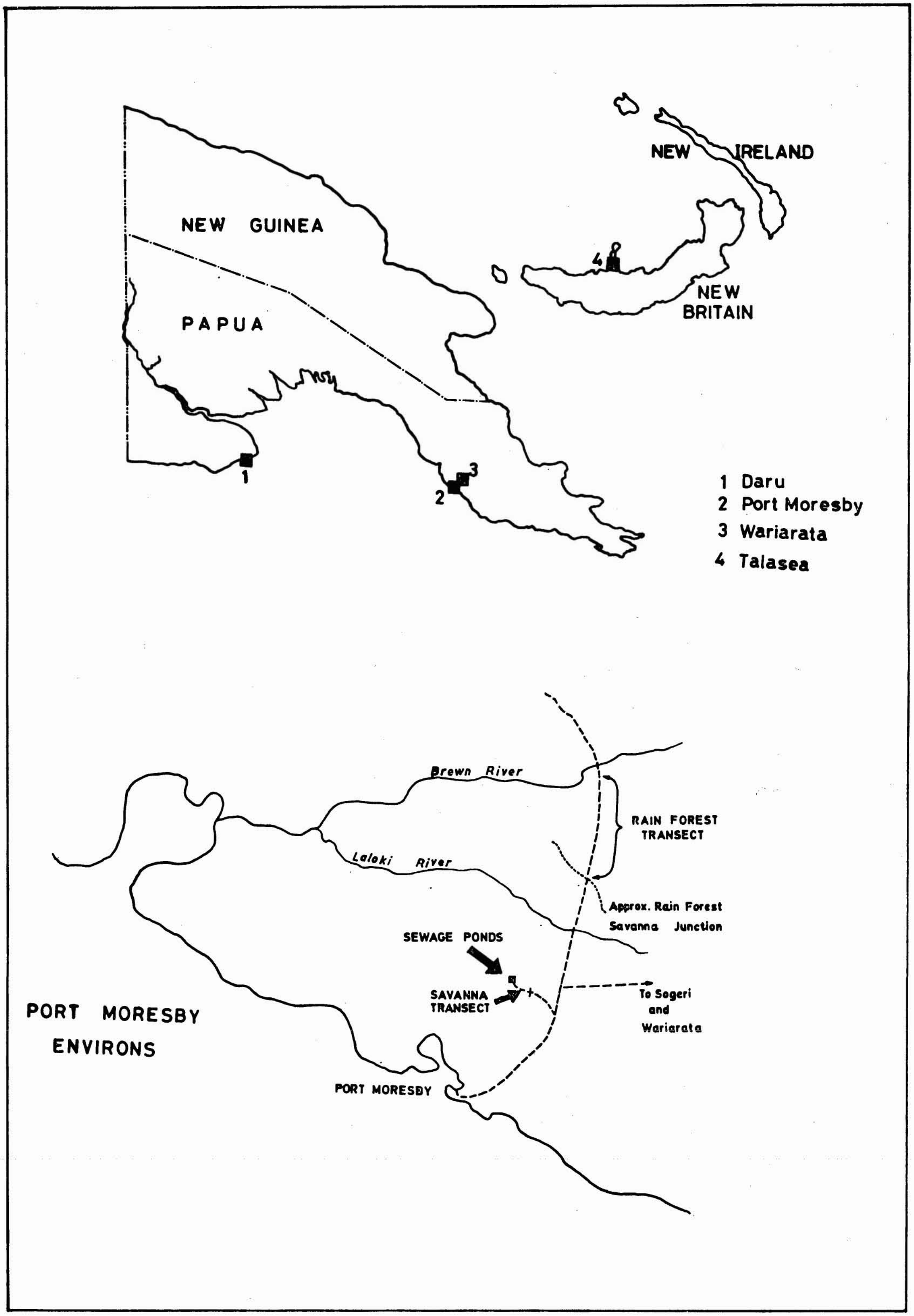

Figure 2. Sampling localities of present study.

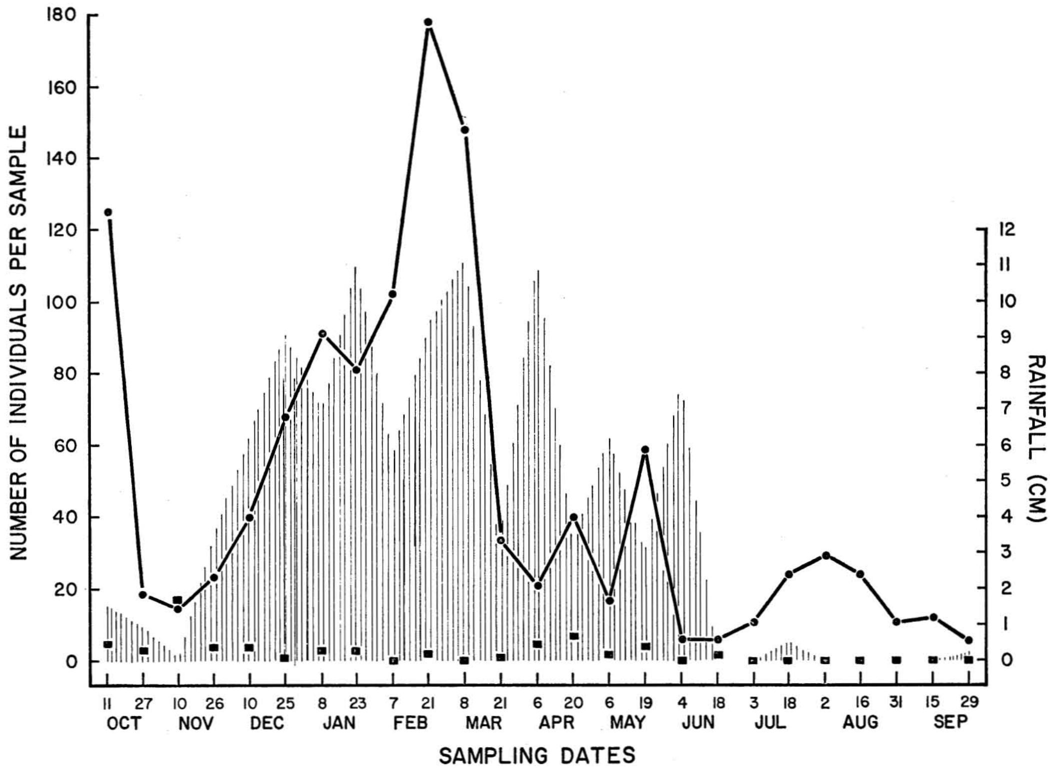

FIGURE 3. Toad census data and total amount of rainfall in 2 weeks preceding the sampling date. Circle, savanna count; square, rain forest count; vertical lines, rainfall.

Moresby. Biweekly samples and counts were taken at each site. Dates of sampling were set to coincide with nights of the quarter moon in order to have all samples collected under approximately equal light intensity and at approximately the same level of activity if toads were following a lunar cycle. All collections at both sites were made at night, usually around 2000 hours. The toads were frozen on the night of collection or on the following morning.

At the savanna site, the number of toads on a 1.6 km (= 1 mile) section of road leading into the sewage plant was counted. Ten males and 10 females were collected from the vicinity of the sewage settling ponds at each sampling period. During the dry season (April through September), 50 toads were collected and the first 10 males and 10 females were processed, this technique being used because of the difficulty in distinguishing the sexes in the field. Larger samples of 50 to 100 individuals were collected at the savanna site in October, February, June, and August for size analyses. Samples were also collected at Daru (Western District), Talasea (West New Britain District), and Wariarata (Central District) (see Figure 2).

At the rain forest site, toads were both counted and collected along a 9.6-km section of the road. This sampling without replacement was done principally on the first 3.2 km of road as toads were rarely seen beyond this initial section of rain forest road. Although the road was patrolled, no toads were obtained from the rain forest site from June to September 1972.

Even though both census transects were along unpaved roads, the toad counts represent censuses of the bordering habitats and not of the road, since the toads were from adjacent areas and were using the roads only as a feeding area. Brattstrom (1962) showed that toads fed at sites other than their diurnal resting sites. The bordering habitats represent a little-disturbed eucalyptus savanna and a seasonal rain forest. The savanna transect did not include the sewage plant as the terminus of the transect was nearly 100 m from the plant. One section (0.4 km) of the rain forest transect passed through a maturing-teak plantation.

The following data were obtained from each toad: snout-vent length, total body weight, total gonad weight, total fat body weight, and stomach content weight. The reproductive condition of each female was recorded. Length measurements were made with dial calipers to the nearest 0.1 mm. Weights were obtained on an electronic balance to the nearest 0.1 g. All stomach contents for a single night from a single sample area were lumped and later analyzed for the weight of animal and plant matter, and the animals were identified to the lowest possible taxon.

TABLE 1

MONTHLY RAINFALL (IN CM) FOR THREE METEOROLOGICAL STATIONS IN THE PORT MORESBY AREA, CENTRAL DISTRICT, OCTOBER 1971 TO SEPTEMBER 1972

MONTH	PORT MORESBY	MT. LAWES	BROWN RIVER
Oct	2.5	14.9	23.7
Nov	6.3	5.6	22.5
Dec	12.6	12.0	15.8
Jan	18.0	3.9	21.7
Feb	29.4	26.2	15.7
Mar	32.4	36.0	49.5
Apr	7.8	7.8	11.6
May	5.7	5.7	6.1
Jun	0.1	0.2	0.0
Jul	0.2	0.0	0.2
Aug	0.0	0.0	0.0
Sep	0.1	0.0	0.4

Relative Abundance

Our method of census can provide only a rough index of population density. Since we were taking a transect count without marking individuals, we were recording only those individuals active on the night of the census; thus, our counts combine both the amount of activity and the density of the population. Certainly the large variation in numbers of toads observed between two adjacent sampling nights (Figure 3) indicates different levels of activity. Brattstrom's homing and recapture data (1962) suggest that an individual toad is not active every night or not feeding at the same place every night, since his toads were returning to a specific feeding site on the average of every 3.6 nights.

In spite of this effect of activity on the censuses, the great disparity of the counts between the two sample areas indicates that toad density of the savanna is many times greater than that of the rain forest. Estimates of density can be obtained either by taking the highest count or by averaging the counts of the entire period of study. The roads were approximately 3.5 m wide, and the savanna census area was 5.6 hectares, and that of the rain forest 11.2 hectares. Thus, the first method yields an estimate of 32 toads per hectare in the savanna and three per hectare in the rain forest. By the second method, there are eight toads per hectare in the savanna and one per 2 hectares in the rain forest. Both estimates indicate that the toad density of the savanna is at least 10 times greater than that of the rain forest.

Lear (1970) estimated the toad density of three sites near the University of Papua New Guinea by a mark-recapture method. His mowed savanna site yielded 15 toads per hectare, and two lawn sites with adjacent buildings and shrubbery yielded 302 and 312 toads per hectare. Lear's savanna density lies between our two estimates, thereby suggesting that toad density in undisturbed savanna is 10 to 30 toads per hectare. In direct contrast, the density around human habitation is many times greater, e.g., Lear's estimate for the campus.

The rainfall for the Port Moresby meteorological station at Jackson Airport is plotted in Figure 3. Rainfall data are presented for the 14 days prior to 26 October 1971 and subsequently for the 14-day interval between sampling dates. Although the sewage plant and the meteorological station are several miles apart, the rainfall at both should be nearly equivalent, as both are savanna and lie in the same valley. By examining Table 1, one can estimate the rainfall of the rain forest site. The site lies between the Mt. Lawes and the Brown River stations but closer to the former. Rainfall at the sampling site should, therefore, be similar but slightly higher than that of Mt. Lawes.

Rainfall is clearly affecting the activity of the toads in the savanna. After the first sampling, the number of toads dropped drastically in association with decreasing rainfall. As rainfall increased and became relatively constant during the northwest monsoon, the number of toads increased. At the rain forest site, the number of toads remained low with the exception of the 10 November sample. This sample was collected during a light rain. The rain may have stimulated increased activity, since the preceding 2 weeks had been very dry.

TABLE 2

MONTHLY MEAN FAT BODY WEIGHTS (IN G) OF *Bufo marinus* FROM THE SAVANNA AND RAIN FOREST SAMPLE SITES, 1971 TO 1972

MONTH	SAVANNA N	SAVANNA ♀♀	RAIN FOREST N	RAIN FOREST ♀♂
Oct	19	0.04	5	0.20
Nov	16	0.01	9	0.64
Dec	20	0.07	4	0.01
Jan	16	0.08	4	0.57
Feb	17	0.18	2	1.80
Mar	15	0.15	1	3.10
Apr	16	0.59	4	0.83
May	19	0.30		—
Jun	20	0.40		—
Jul	20	0.08		—
Aug	31	0.05		—
Sep	20	0.03		—

Sexual Dimorphism

Sexually mature and sexually active *B. marinus* are sexually dimorphic. Males are dorsally a uniform cinnamon brown and strongly spinose, as each wart is capped by a short horny spine. Their thumbs are slightly enlarged at the base and bear a dark keratinous pad on the dorsal surface. Females have a mottled dorsum. The dorsal ground color tends to be an olive brown interrupted by an irregular middorsal beige stripe. Dorsolaterally and laterally, small irregular beige spots are interspersed among large grayish brown spots. The thumbs have no keratinous pads and are cream-colored dorsally. This female pattern is a retention of the juvenile pattern and is also evident in sexually immature or quiescent males. Inger (1954) noted a similar sexual dimorphism in *B. marinus* in the Philippines. There is no size difference between the two sexes (Figure 4).

Reproduction

Testicular weights and lengths were recorded for the first 3 months of this study. However, a preliminary analysis of these data failed to provide any criteria for the determination of reproductive state; thus, the recording of these data was discontinued.

The proportion of ovary to body weight can be used to differentiate five reproductive stages. Proportional values (body weight: ovary weight) greater than 200 are associated with empty ovaries, between 200 and 100 with the development of ova, between 100 and 65 with the initial yolking of ova, between 65 and 30 with the beginning of pigmentation, and 30 or less with fully yolked and pigmented ova, i.e., the gravid state. These limits were not arbitrarily selected. The proportions were calculated and grouped according to the observed reproductive condition. Less than 10 percent of the proportions failed to agree with the proportional classes, and these were borderline cases. Thus, the proportional classes accurately reflect the five observed reproductive states of *Bufo marinus* for the Port Moresby area.

A survey of the females' reproductive state for each month is presented in Figure 5. A portion of the female population possesses eggs ready for deposition in each month. Field observations support the continual reproductive readiness of *B. marinus*, for any heavy afternoon or evening rainfall would bring forth breeding aggregations.

The proportion of gravid females seems to be determined, at least in part, by the frequency and heaviness of local rainfall. Wilhoft (1965) suggested a similar phenomena for *B. marinus* in Australia. Heavy rainfall preceding the sampling date will reduce the number of gravid females. For example, reduced rainfall in October 1971 prevented breeding, so that nearly 60 percent of the November females were gravid. With the onset of the monsoon in late November, the number of heavy showers increased through December, and the January sample was reduced to 25-percent gravid females. Although the proportion of gravid

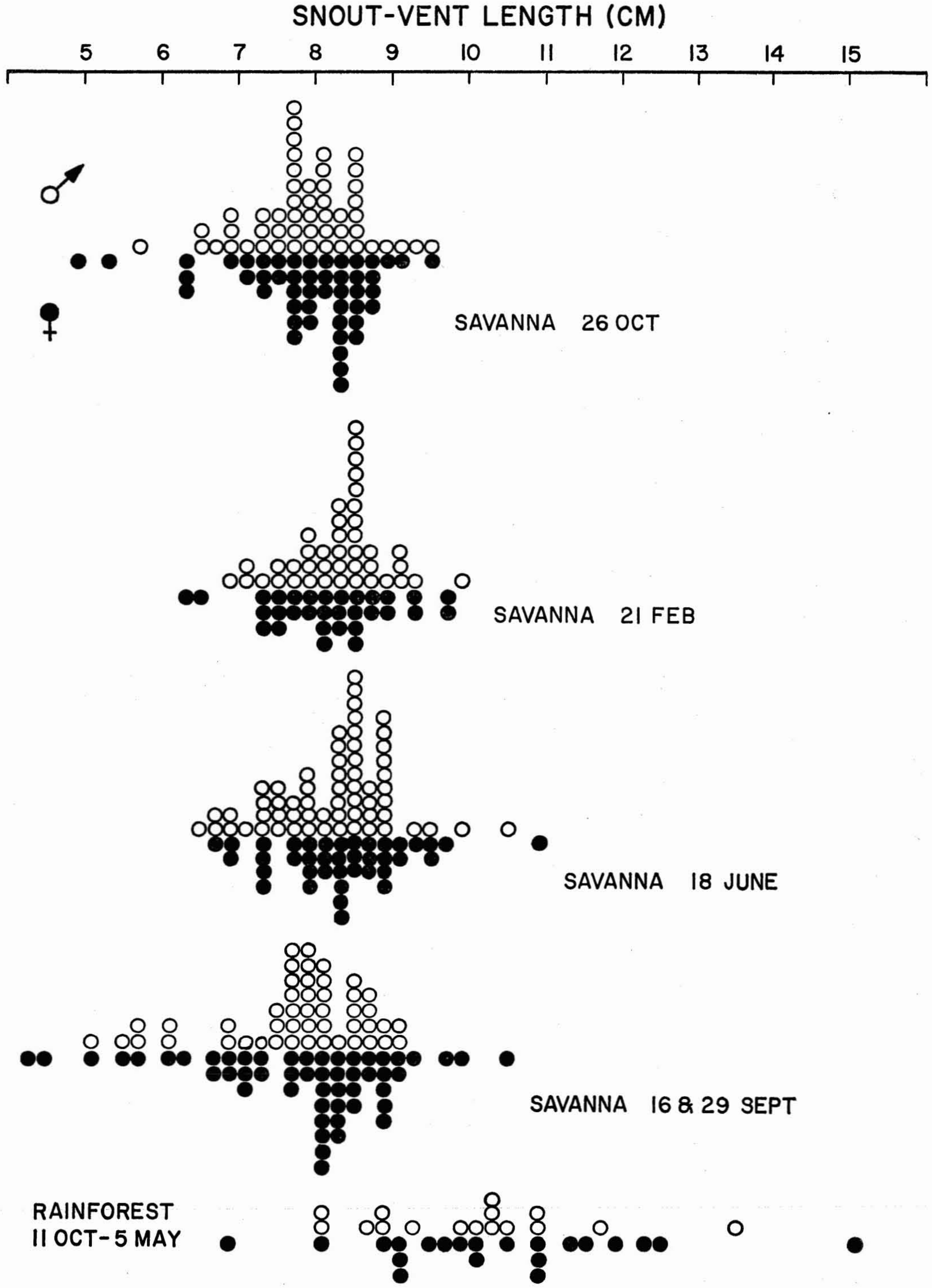

Figure 4. Female and male size distribution of *Bufo marinus* for Port Moresby area samples. Each circle represents one toad.

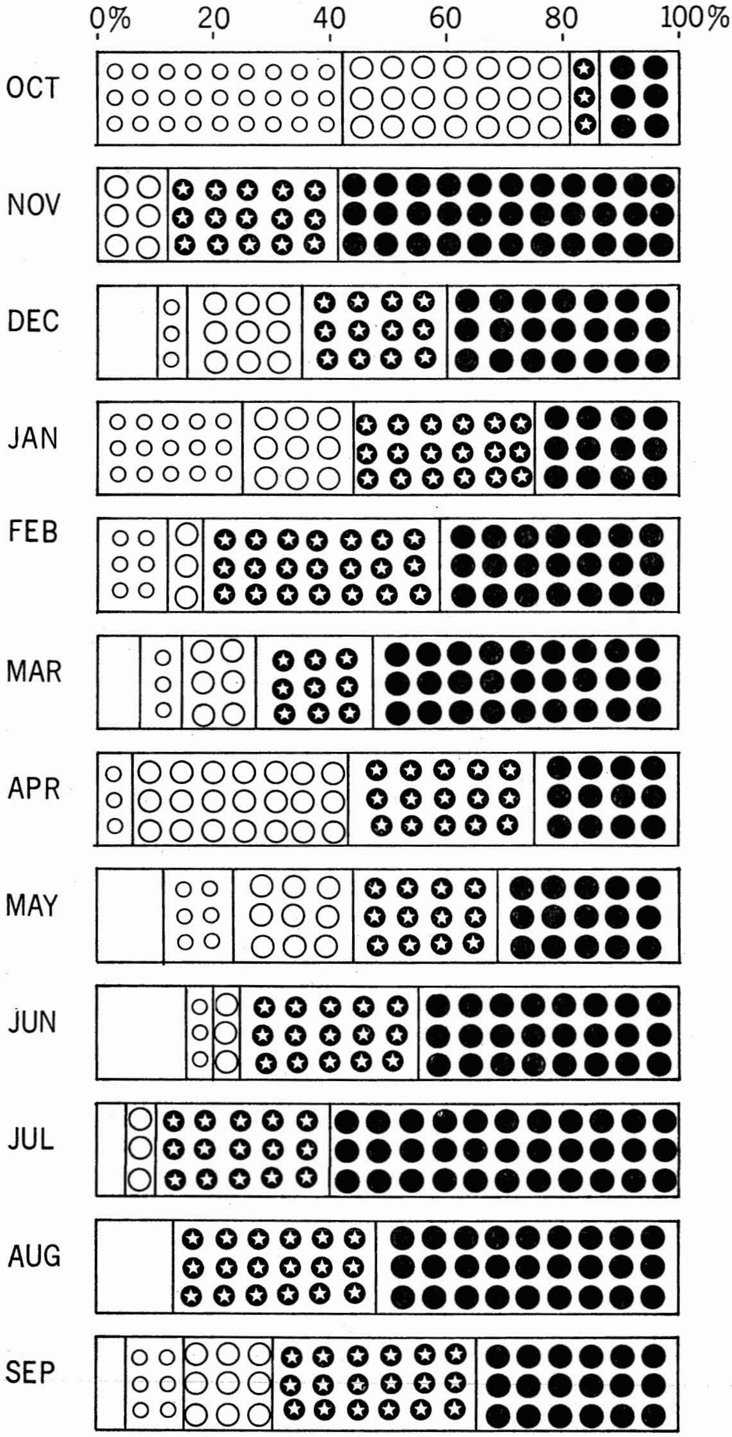

FIGURE 5. Reproduction condition for savanna sample of female *Bufo marinus* showing percent of females in the five reproductive classes. Solid circles, ova fully yolked and pigmented; circle enclosing star, ova beginning pigmentation; large open circle, ova beginning to yolk; small open circle, development of ova; blank, ova absent or not visible.

TABLE 3

Comparison of the Regression Parameters ($Y = xb + a$) of Weight on Snout-Vent Length

DATE	N	x	Y	s_x	b	a	S_{yx}	r
Savanna								
26 Oct 71	99	7.79	3.46	0.18	0.434	0.083	0.001	0.97
21 Feb 72	72	8.12	3.74	0.16	0.125	2.73	0.008	0.47
19 Jun 72	100	8.30	3.79	0.14	0.355	0.842	0.003	0.88
19 Jul 72	51	8.18	3.67	0.18	0.232	1.770	0.016	0.66
17 Aug 72	52	7.73	3.45	0.17	0.424	0.172	0.004	0.93
16 Sep 72	50	8.12	3.68	0.09	0.437	0.135	0.008	0.86
15 Oct 72	48	8.01	3.63	0.09	0.431	0.173	0.005	0.90
Rain Forest								
Oct–Apr	37	10.19	4.67	0.16	0.545	−0.885	0.005	0.97

Note: N, sample size; x, mean snout-vent length (cm); Y, mean of cube root of body weight (g); s_x, standard deviation of mean snout-vent length; b, slope regression line; a, Y-intercept of regression line; S_{yx}, standard deviation of regression coefficient; r, linear correlation coefficient.

females each month seems to be related to rainfall, newly gravid individuals appear each month. Each monthly sample possesses females in different stages of oogenesis. The lack of rainfall and, thus, the lack of egg deposition reduce the number of females with early oogenic stages; e.g., November, July, and August in Figure 5.

We lack data on the length of the reproductive cycle for individual females. There is no means of determining from our data whether a female will produce one or more clutches per year. We suspect that within the savanna population a female will produce only one clutch of eggs per year. The lack of well-developed fat bodies suggests a slow maturation of ova. Table 2 shows the difference in size of fat bodies for the savanna and rain forest samples. The fat bodies in the savanna sample were usually small, less than 0.1 g for all specimens—male or female, and for females at all reproductive stages. The rain forest sample had larger fat bodies. However, in neither sample is there any indication of a fat body cycle associated with the reproductive cycle. Such a cycle, if it exists, will be evident in the better-fed rain forest population.

The presence of gravid females in each monthly sample clearly indicates that *Bufo marinus* is an opportunistic breeder. Observations on the external sexual characters of males suggest that, unlike the female, the male population tends to be more cyclic, and the majority of adult males reaches reproductive peak at the beginning of the monsoon. This interpretation results from the ease of sexing adult toads in October through December. From January through September, some adult males in each sample were consistently mistaken for females, because these males had lost their keratinous nuptial pads and had assumed the females' mottled color pattern.

Size and Sex Distribution

Our samples from the rain forest and savanna sites were composed of subadults and adults. Postmetamorphic individuals and juveniles were not purposely avoided. Individuals of these age classes either did not occur at the sampling sites or were there in such small numbers that they were neither observed nor collected.

Rain forest toads are larger and heavier than are the savanna toads. Comparison of body length (Table 3 and Figure 4) shows that on the average a rain forest toad is 2 cm longer and 50 g heavier than a savanna toad. The difference in length is significant, i.e., two times the standard error of the mean plus or minus the means produce no overlap. Because the rain forest toads were longer, their average weight was greater; however, the difference between the two samples reflects also a proportional difference. If the two samples with low linear correlation coefficients (February and July samples of Table 3) are ignored, then the slopes of the regressions show that the weight of savanna toads increases at the rate of 0.42 $g^{\frac{1}{3}}$ per cm;

TABLE 4

COMPARISON OF THE DIET OF THE SAVANNA AND RAIN FOREST SAMPLES

	SAVANNA		RAIN FOREST	
SAMPLING DATE	GRAMS FOOD PER INDIVIDUAL	PERCENTAGE OF ANIMAL MATTER IN FOOD	GRAMS FOOD PER INDIVIDUAL	PERCENTAGE OF ANIMAL MATTER IN FOOD
1971				
11 Oct	0.10	—	5.50	—
26 Oct	0.31	42	—	—
11 Nov	0.17	18	1.30	75
25 Nov	0.80	65	5.30	—
7 Dec	1.84	91	3.00	92
20 Dec	0.68	72	3.70	89
1972				
9 Jan	1.17	15	2.20	49
23 Jan	0.77	27	11.40	99
7 Feb	0.98	53	—	—
21 Feb	1.84	64	3.00	70
8 Mar	1.09	94	—	—
21 Mar	0.73	—	15.00	—
6 Apr	0.80	77	0.80	92
20 Apr	0.72	72	2.10	90
6 May	0.94	79	4.00	100

whereas that of the rain forest toads increases at 0.54 $g^{\frac{1}{3}}$ per cm. This difference was apparent when the former were collected, since they were emaciated and, in fact, appeared to be starving.

In neither the rain forest nor the savanna sample was there any evidence of a size difference between females and males (Figure 4). The 26 October and 16 and 29 September savanna samples indicate a one-to-one relationship between the sexes, 49 females:51 males and 52:47, respectively. The other two savanna samples, 31:41 and 39:61, show a predominance of males, and chi-square values of 0.698 and 2.450 require the rejection of a one-to-one relationship. The rain forest sample with 16:21 is marginally acceptable as a population of equivalent number of sexes (chi-square 0.335).

Feeding Habits

The differences in mean body length and weight of the savanna and rain forest samples suggest a difference in the level of nutrition between the two populations. That such a difference does exist is shown in Table 4. Between October and May, a rain forest toad had on the average 4.78 g of food in its stomach; and, of this food, 84 percent consisted of animals. In contrast, a savanna toad during this same period had an average 0.86 g stomach content of which 59 percent was animal matter. On a yearly basis (Table 5, Figure 5), rain forest toads have a greater stomach content and a larger portion of it is animal matter than is that of the October to May savanna sample. Even if individuals with empty stomachs are excluded from the calculations, the savanna toads still have only 1.13 grams of food per individual, a third that of the rain forest toads. Thus, the daily diet of the rain forest toads contains not only more food, but a larger portion of this food is proteinaceous. The large amount of plant matter in the stomachs of savanna toads indicates that they were actively eating pieces of plants and not accidentally ingesting plants with animal prey.

Three extralimital samples (see Figure 2) from Wariarata (rural savanna; Central District), Daru (urban savanna; Western District), and Talasea (rain forest margin; West New Britain District) show similar dietary phenomena between disturbed and undisturbed habitats. The Talasea and Wariarata samples were drawn from less disturbed habitats than the sample from the town of Daru. Studies

TABLE 5

ANALYSIS OF STOMACH CONTENT DATA OF THE SAVANNA SAMPLE

DATE	N	N_o	TOTAL WEIGHT OF STOMACH CONTENTS	MEAN WEIGHT OF STOMACH CONTENTS EXCLUDING EMPTY ONES	STOMACH CONTENTS	
					WEIGHT OF ANIMAL MATTER	WEIGHT OF PLANT MATTER
1971						
11 Oct	18	15	1.9	0.60	—	—
26 Oct	20	0	6.3	0.32	2.7	3.6
11 Nov	19	8	3.3	0.30	0.6	2.7
25 Nov	16	2	12.7	0.91	8.2	4.5
7 Dec	20	0	37.0	1.85	34.0	3.0
20 Dec	19	2	12.9	0.76	9.2	3.7
1972						
9 Jan	20	0	23.4	1.16	3.7	19.7
23 Jan	16	1	12.4	0.83	3.4	9.0
7 Feb	17	0	16.7	0.98	8.8	7.9
21 Feb	20	0	36.9	1.84	23.6	13.3
8 Mar	15	3	16.4	1.37	15.4	1.0
21 Mar	20	1	14.6	0.77	—	—
6 Apr	16	3	12.8	0.98	9.8	3.0
20 Apr	20	4	14.5	0.91	10.5	4.0
6 May	20	3	18.9	1.11	15.0	3.9
19 May	20	1	40.3	2.12	30.0	10.3
4 Jun	20	4	18.2	1.14	15.9	2.3
18 Jun	20	9	13.7	1.25	6.1	7.6
3 Jul	20	9	14.8	1.35	11.0	3.8
18 Jul	20	13	18.1	2.59	6.1	2.0
2 Aug	20	12	5.5	0.69	4.2	1.3
16 Aug	20	7	7.3	0.56	4.7	2.6
31 Aug	20	12	8.1	1.01	7.1	1.0
15 Sep	20	6	14.0	1.17	12.9	1.1
29 Sep	20	2	27.9	1.55	22.0	5.9
Year's Mean	19	5	16.3	1.13	11.5	5.1

NOTE: Weights in grams. N, number in sample; N_o, number in sample with empty stomachs.

from the first two areas show average grams of food per toad as 3.99 and 2.06, respectively, and the Daru sample as 0.68. The proportion of animal matter is 92, 68, and 84 percent, respectively. Talasea is the most forested locality and, as in the Brown River Road sample, exceeds the two savanna samples in total amount of food and percentage of animal matter.

The identity and relative numbers of animal prey are given in Appendices 2 to 4. At a higher level of comparison (Table 6), it is apparent that *B. marinus* will eat just about anything it can catch.

Economic Importance

Our analysis of stomach contents shows that *Bufo marinus* is not a selective feeder but eats a variety of animate and inanimate material. Young toads have been found in the stomachs of adults from Daru; Simmonds (1957) previously reported cannibalism in Fiji toads. Like the marine toads in Florida (Alexander 1965), toads in Post Moreby feed on vegetable matter and on dog and cat food. Their feeding on the latter food shows that stationary food can be located and suggests that *B. marinus* actively eats vegetable matter. However, whether nutrition is obtained by this ingestion of vegetable matter is unknown.

TABLE 6

COMPARISON OF ANIMAL PREY IN *Bufo marinus* AT FIVE LOCALITIES IN PAPUA NEW GUINEA

TAXA	PORT MORESBY SAVANNA (480)	PORT MORESBY RAIN FOREST (31)	WARIARATA SAVANNA (17)	DARU SAVANNA (90)	TALASEA RAIN FOREST (31)
Annelida	.	×	.	.	.
Gastropoda	×	.	.	×	×
Arthropoda					
(non Insecta)	×	×	×	.	×
Insecta					
Blattodea	×	×	.	.	.
Isoptera	×	.	.	.	.
Mantodea	.	.	×	.	.
Dermaptera	×	.	.	.	.
Orthoptera	×	×	×	×	×
Hemiptera	×	×	×	.	×
Coleoptera	×	×	×	×	×
Diptera	×	.	.	×	.
Lepidoptera	×	×	×	×	.
Hymenoptera	×	×	×	×	.
Chordata	.	.	.	×	.

NOTE: Numerals in parentheses indicate sample size.

Only Dexter (1932) and Wolcott (1937) have truly attempted to evaluate the marine toad as a biological control agent. *B. marinus* was introduced into Puerto Rico to control the scarabaeid beetles in sugarcane fields. They collected toads from cane fields and noted that scarabaeid beetles were the principal food item; thus, they concluded that the toads were effective biological control agents. Other researchers (Fellows 1969, Hinckley 1963, Illingworth 1941, Pemberton 1934) have commented on the economic importance of these toads and, on the basis of diet, have considered them economically neutral. Because our samples are from nonagricultural areas, we have no suitable base to evaluate the economic value of the toad's diet in the Port Moresby area. Certainly the reduced diet of the sewage plant toads suggests that they have reduced the populations of terrestrial or low-flying insects. On the negative side, their great abundance creates minor traffic hazards and a general nuisance around human habitation.

One interesting point arose during our inquiries into the spread of *B. marinus*. Planters and sawmill operators stated that, since the coming of the toad in their areas, the number of mosquitoes had markedly decreased. Further investigation of this assertion is required since it contradicts the statement that the tadpoles eat algae but not prawns or mosquito larvae (Turbot 1938).

Competition

New Guinea has no native *Bufo*, bufonid, or any ecological anuran equivalent to *Bufo marinus*. The savanna anuran species of the Port Moresby area are arboreal: *Litoria congenita*, *L. caerulea*, *L. infrafrenata*, *L. bicolor*, and *L. impura*; or, if terrestrial, they are closely associated with water: *Rana papua* and *Litoria nasuta*. Considering these differences in habits and habitats, we doubt if the adult native frogs are in competition with *Bufo marinus*. Although competition may exist between the tadpoles, we believe that habitat alterations by man are more likely to create unsuitable spawning sites for the native frogs. Tadpoles of the marine toad can tolerate water temperatures as high as 42° C (Krakauer 1970) and develop rapidly, e.g., 6 to 8 weeks (Alcala 1957, Sein 1937); thus, they can survive in man-modified spawning sites. Field observation by Lindgren supports the concept of euroythermic superiority of *B. marinus* tadpoles in such spawnings sites. During the dry season, the creeks around Port Moresby became divided into a series of isolated pools, which became quite warm. Toad tadpoles and fingerlings of the introduced *Tilapia* were swimming and feeding normally, while the native fishes (*Melanotaenia*, *Mogurnda mogurnda*, and *Meosilurus*) were dying because of heat prostration or a lack of oxygen.

Predators

There is so far no evidence that the subadult and adult toads are a prey item for any New Guinean animal. Only one adult toad was found that may have been attacked by a natural predator. This toad possessed deep lacerations on the body and head; apparently it was killed by a barn owl but was not eaten. Postmetamorphic and juvenile toads may be preyed upon by subadults and adult toads.

There are no reports of predation on adult marine toads within their natural range. In contrast, within their introduced range, the following mammalian predators have been reported: *Rattus rattus* (Adams 1967), mongooses (Baldwin, Schwartz, and Schwartz 1952), rats (Cassels 1966, St. Cloud 1966), dogs and cats (Krakauer 1968); avian predators: Australian koel (Cassels 1970), chickens (Oliver and Shaw 1953), birds (Straughan 1966); reptilian predators: *Candoia* (Gorham 1968), *Varanus salvator* (Alcala 1957).

Résumé

Bufo marinus was apparently introduced onto the main island of New Guinea in the late 1930s. In areas of savanna, such as the Port Moresby area, and of man-disturbed habitats, the toads have been able to disperse naturally. However, rain forest, swamps, and rivers have apparently acted as dispersal barriers, so that the introduction of the toads into new areas has been through human transport.

The marine toad will undoubtedly continue to spread throughout New Guinea. We suspect that it will gain a stronger foothold in the highly agriculturally modified highlands. The Fly River delta and the area to the west appear to be a prime region for toad expansion. It is both surprising and fortunate that they have not yet been carried from Daru to this area.

The density of toads in the savanna exceeds that of the rain forest margin by approximately 10 times. Lear's (1970) data show that the urban populations are again 10 times that of the savanna. On the average, we would expect the following relationships: 3 toads per hectare along the forest margin, 30 in savanna, and 300 in towns.

Toad activity is strongly influenced by rainfall. If there are frequent rains, it appears that most of the members of a population will be active on any given night. As rainfall decreases, fewer and fewer individuals will be active on a given night. Perhaps a portion of the population becomes dormant during these dry periods.

In New Guinea, *B. marinus* is an opportunistic breeder with at least 10 percent of the females prepared to breed in any month. The secondary sexual characters of the male toads indicate a peak breeding season from October through January. This period coincides with the beginning of the monsoon season, and we wonder whether this peak breeding phenomenon is a local adaptation of the Port Moresby toads.

Rain forest toads are larger than savanna toads. The greater density in the savanna may be a factor reducing the average food intake per toad. Certainly the savanna toads had, on an average, less food in their stomachs and a lower percentage of animal or proteinaceous matter. This dietary difference could explain the smaller size and emaciated condition of the savanna toads.

There is presently no evidence of competition between *B. marinus* and the native savanna frogs or displacement of the latter. The toad tadpole can tolerate the high water temperature of manmade pools and puddles and thus has a selective advantage over the native frogs in the urban situation. Likewise, we found no evidence that any New Guinean animal is using the toads as food.

SYNOPSIS OF *Bufo marinus* ECOLOGY

Within its natural range (Central America and the northern half of South America), *Bufo* *marinus* occurs primarily around human habitation, in savannas and open forests such as riparian, broadleaf, and scrub (Duellman 1963, 1965; Stuart 1950). Stuart believes that the rain forest acts as a dispersal barrier for the toad in Guatemala; Alcala (1957) expressed a similar opinion for the Philippine rain forest. As a general observation, it would appear that the toad's density is low in all areas except around human habitation; in fact, Heatwole (1966) noted their rarity everywhere in Panama but around houses. Except for our numerical estimate of density and that of Lear (1970), no other investigators have given more than the subjective categories of rare, uncommon, abundant, etc., as density estimates.

Accurate density figures are needed to evaluate the marine toad's trophic position in its natural and, particularly, in its introduced communities. Where introduced, it rapidly becomes the visually most abundant anuran. For example, 148 toads were released in Oahu, Hawaii, in April 1932; by July 1934, 103,517 juvenile toads had been removed from the site of original introduction to other locations on the island (Pemberton 1934). This ability for a rapid increase in population can largely explain *B. marinus*'s success as a colonizer. Likewise, the rapid obtainment and maintenance of high density have undoubtedly modified the trophic structure of the communities into which it was introduced.

B. marinus has an *r* reproductive pattern (sensu MacArthur and Wilson 1967). A gravid female contains from 8,000 to 35,000 eggs (Oliver 1949, Straughan 1966), which are deposited during one breeding period. An individual female probably breeds once a year (Pemberton 1934), although this assumption needs confirmation. *Bufo marinus* is capable of year-around breeding in most areas (see figure 3 in Honegger 1970, and our Figure 4), although this capacity is not realized in many areas owing to climatic factors, e.g., no breeding because of low temperatures and/or absence of rainfall (Krakauer 1968, Straughan 1966, Wingate 1965). Breeding sites can be either in temporary or permanent bodies of water (Alcala 1955, Stuart 1950).

Once laid, the eggs will probably not be eaten, since they appear to be toxic (Licht 1967). The eggs and tadpoles tolerate low concentrations of seawater (Ely 1944) and water temperatures from 10° to 42° C (Krakauer 1970). Upon hatching, the tadpoles form schools and are distasteful (Wassersug 1973); both factors increase the tadpoles' survival. The larval period is relatively short, varying from 1 to 3 months depending upon local climatic conditions (Alcala 1957, Oliver 1949, Pemberton 1934, Sein 1937, Straughan 1966). Straughan has shown that in Queensland, Australia, the tadpoles double their body length in the 80 days between commencement of feeding and metamorphism. The *B. marinus* toadlet at the end of metamorphism is 6 to 12 mm long. Growth is rapid, at least in Hawaii, for at 3 months the toad is 60 to 75 mm long and at 6 months, 90 to 120 mm long (Pemberton 1934). If reproductive maturity of marine toads is closely associated with size, these Hawaiian toads have reached sexual maturity in 6 months.

Neither the average life span of adult toads nor the age structure of a marine toad population is known. General observations suggest that, except for periods of metamorphism, toad populations are largely composed of adults. During metamorphism, the banks of ponds and streams are covered with thousands of toadlets. Apparently these postmetamorphic and later juvenile stages suffer high mortality or, at least, they appear to be the vulnerable stages. Other than the few predators noted above, we know little about predators, particularly for tadpoles and juveniles. Similarly we lack data on other mortality factors such as parasites, desiccation, or low food availability.

If we know nothing else about marine toads, we do know the dietary habits of adults. A large number of investigators has demonstrated the catholic diet of marine toads (Dexter 1932, Hinckley 1963, Illingworth 1941, Lever 1945, Rabor 1952, Straughan 1966, Wolcott 1937). They eat the full spectrum of arthropods and small vertebrates.

ACKNOWLEDGMENTS

We wish to thank the Department of Agriculture, Stock and Fisheries of Papua New Guinea for the use of its Wildlife Laboratory facilities and the encouragement and aid provided by its personnel. Mr. Fenner and Dr. Stibbick of the D.A.S.F. Entomology Division were of utmost help in the identification of the insects. One of us (G.R.Z.) was supported by a grant from the Smithsonian Research Foundation.

APPENDIX 1

DISTRIBUTION OF *Bufo marinus* ARRANGED BY POLITICAL DISTRICTS OF PAPUA NEW GUINEA

BOUGAINVILLE: Present at Bana (1945), Bain, Buka, Hutjena (1938), Kieta (1955), Konga (1959), Kongora (1959), Kono (1967), Kuba (1940), Lugakai, Makis (1967), Mortlock Island, Pangana, Selau (1940), Sohano (1952), Torokina (1970), Wakunai (1940); absent at Baitsi, Kunua.

CENTRAL: Present at Bolu Bolu (1966), Itikinumu (1969), Kwikila (1972), Lea Lea, Mageri (1964), Marshall Lagoon—west side (1971), Port Moresby, Rigo, Tapini, Tubusereia, Veimauri (1971); absent at Abau, Amazon Bay, Bereina, Cape Rodney, Viefa'a, Waima, Woitape.

CHIMBU: Absent at Chauve, Gembogi, Kundiawa, Mount Wilhelm, Munina, Papnigi; conflicting reports for Kerowagi.

EAST NEW BRITAIN: Present at Amir Island, Balanataman, Kait (1963), Keravat (1938), Kokopo, Rabaul (1945–1948), Stockholm (1960), Vadal (1942–1945), Vunamami, Warangoi; absent at Malmal, Unea Island, Uvol.

EAST SEPIK: Present at Dagua (1968), Dreikikir (1962), Marienberg, Saussi; absent at Angoram, Balif, Kaugia, Yangoru, Wosera; conflicting reports for Kaup, Wewak.

EASTERN HIGHLANDS: Present at Goroko; absent at Agotu, Aiyura, Asaro, Bena Bena, Henganop, Iro'orka, Kainantu, Korofeigu, Lamari, Lufa, Magitu, Okapa, Watabung; conflicting reports for Amaiyufa (1971), Kama Village, Namata.

GULF: Absent at Hevoro, Hoe, Ihu, Karaulti, Kerema, Malalaua, Moru.

MADANG: Present at Alexishafen, Kar Kar Island (1958), Madang (1960), Saidor (1970), Wararuk (1961); absent at Aiome, Awar, Bundy, Chungribu, Crown Island, Dumpu, Gogol, Josephstaal, Long Island, Manam Island, Mikarew, Mirap, Simbai, Usino, Yauar; conflicting reports for Bogia, Nodobu.

MANUS: Present at Baluan Island, Lawes (1972), Lorengau (1942–1945), Lugus, M'bunai, Malai Bay, Mokerang (1942–1945), Sau; absent at Derimbat, Lessau, Pam Island, Rambutyo.

MILNE BAY: Present at Alotau (1951), Bubuleta, Dogura (1965), Esa Ala (1945), Fife Bay, Kwakwela (1942–1945), Normanby Island (1970), Rabaraba, Rabe, Sagarai (1942–1945), Samarai (1942–1945); absent at Agaun, Baniara, Damena, Fergusson Island, Goodenough Island, Losuia, Misima Island, Rossel Island.

MOROBE: Present at Bubia (1942–1945), Bulolo, Huon (1964–1967), Kaiapit (1967), Kasanombe (1960s), Lae, Mumeng (1969), Munum, Rooke Island, Situm (1962), Wau (1942–1945); absent at Finschhafen, Kabwum, Menyamyai, Pindui, Siassi Island, Wantoat.

NEW IRELAND: Present at Baugung, Emira Island, Kavieng (1942–1945), Konos, Lakuramau, Lambon, Lavongai, Lungatang, Metekabil, Meteran, Nalikaria (1942–1945), Namatanai, Paus, Taskul; absent at Mussan Island, Noipaus, Tench Island, Umbukul.

NORTHERN: Present at Eroro, Gona, Higaturu (1963–1965), Isivina, Musa (1966–1967), Popondetta (1966), Sangara (1970); absent at Afore, Gorori, Ilimo, Ioma, Kikinonda, Kokoda, Manau, Pongani, Sila, Wanigela.

SOUTHERN HIGHLANDS: Absent at Bela, Erave, Ia ibu, Kagua, Kiburu, Komo, Lake Kutubu, Margarima, Mendi, Nipa, Pangia, Poroma, Samberigi, Talnggi, Tari.

WEST NEW BRITAIN: Present at Bali (1970), Evassi (1942–1943), Garu, Gloucester, Hoskins, Kwalakessi, Nakanai (1954), Sag Sag, Talasea, Wita Island; absent at Kandrian, Saiho.

WEST SEPIK: Present at Pes, Yalangi River; absent at Aitape, Amanab, Fatima, Green River, Lumi, Ossima, Yangkok; conflicting reports for Nuka, Nukuanglo, Vanimo.

WESTERN DISTRICT: Present at Daru; absent at Aewe, Awaba, Balimo, Bulumuk, Kawito, Kianga, Lake Murray, Morehead, Oriomo, Suki, Weam.

WESTERN HIGHLANDS: Present at lower Jimi Valley (1971), Kauapena, Rulna (1972), Tabibuga, Tambul (1970); absent at Baiyer River, Banz, Kandep, Koinabe, Kompian, Kuk, Kunder, Minj, Mondomil, Mount Hagen, Porgera, Wapenamanda, Warbag; conflicting reports for Tsigmil (1940).

NOTE: The localities are those from which an answered questionnaire was returned. Date in parentheses is the correspondent's estimate of date of toad's introduction.

APPENDIX 2

IDENTITY AND NUMBER OF PREY OF THE *Bufo marinus* FROM THE SAVANNA SAMPLING SITE

MOLLUSCA

Gastropoda—24 small forest snails

ARTHROPODA

Chilopoda—10 centipedes

Diplopoda—16 millipedes

Arachnida
- Araneae—25 spiders
- Acarina—1 tick

Isopoda—1 slater

Insecta
- Blattoda
  - Blattidae—7 cockroaches including 3 *Periplaneta grunnea* and 1 *Periplaneta americana*
- Isoptera—800 termites
- Dermoptera—3 earwigs
- Orthoptera
  - Gryllidae—40 *Acheta commoda*
  - Gryllotalpidae—3 *Gryllotalpa africana*
  - Pyrgomorphidae—11 *Desmoptera* sp.
  - Acrididae—4 short-horned grasshoppers
- Hemiptera (116 bugs total)
  - Cicadellida—4 leafhoppers
  - Miridae—8
  - Reduviidae—5 assassin bugs
  - Pentatomidae—19 shield bugs
  - Cydnidae—51 *Adrisa* sp.
- Coleoptera
  - Carabidae—22 ground beetles
  - Dytiscidae—1 water beetle
  - Curculionidae—19 weevils including 8 *Apion* sp., 3 *Cylas formicarius*, 2 *Oribus* sp., 2 *Cryptorhinus* sp., and 1 *Pachyrhynchinis* sp.
  - Elateridae—11 click beetles including 5 *Lacon* sp., and 3 *Aeolis* sp.

Tenebrionidae—12
Lagriidae—3
Anthicidae—1
Othniidae—1
Cerambycidae—7 unidentifiable longhorns
Chrysomelidae—41 leaf beetles including 1 species of Cassidae
Heterocidae—4
Hydrophilidae—11 water beetles
Scarabaeidae—21 including 1 *Melolontha* sp. and 16 *Hybosorinas* spp.
Staphylinidae—4 rove beetles and 1 larva
Erotylidae—1 fungus beetle
Coccindellidae—10 ladybug beetles

Diptera—12 flies including 5 Muscidae

Lepidoptera—75 unidentified moths and 94 larvae including those listed below
Geometridae—35 looper caterpillars
Nymphalidae—1 *Hypolimnas* sp. caterpillar

Hymenoptera
Vespoidae—2 wasps
Sphecidae—1 *Sphex* sp.
Formicidae—680 ants including 269 *Polyrhachis* sp., 197 *Pheidole* sp., 81 *Oecophylla amaragdina*, and 68 *Odontomachus* sp.

Note: Prey derived from all the toads (476) collected during the biweekly sampling of October 1971 through September 1972.

APPENDIX 3

Identity and Number of Prey of the *Bufo marinus* from the Rain Forest Sampling Site

ANNELIDA

Oligochaeta
Terricolae—3 earthworms

ARTHROPODA

Diploda—28 millipedes

Arachnida
Araneae—2 spiders

Scorpiones
Scorpionidae—1 scorpion

Insecta
Blattodea
Blattidae—1 cockroach

Dermaptera—1 earwig

Hemiptera
Cicadidae—1 cicada
Miridae—1
Coreidae—4
Scutelleridae—2 Harlequin bugs
Pentatomidae—5 shield bugs
Cydnidae—2 *Adrisa* sp.
Gerridae—1 water strider

Coleoptera
  Cicindelidae—1 *Tricondyla aptera*
  Hydrophilidae—3 water beetles
  Curculionidae—49 weevils including 28 *Meroleptus squalidus*, 2 *Rhinoscapha funigris*, 1 *Rhabdoscernus obscurus*, 7 *Cryptorhinus* sp., and 2 *Oribus* sp.
  Elateridae—11 click beetles including 7 *Lacon* sp.
  Cerambycidae—12 unidentified longhorns
  Chyrosomelidae—4 leaf-eating beetles
  Byrrhidae—19 pill beetles
  Scarabaeidae—33 including 9 *Lepidiota* sp., 6 *Melolonthus* sp., and 16 Hybosorinae
  Passalidae—1
  Trogidae—1 carrion beetle
  Geotrupidae—1 dung beetle
  Staphylinidae—7 rove beetles
  Erotylidae—1 fungus beetle

Lepidoptera
  Geometridae—11 unidentifiable larvae and 18 geometrid larvae

Hymenoptera
  Ichneumonidae—10 parasitic wasps
  Formicidae—366 ants including 169 *Odentomachus* sp., 123 *Pheidole megacephala*, and 22 *Oecophylla smargadina*

NOTE: Prey derived from all the toads (37) collected during the biweekly sampling of October 1971 through May 1972.

APPENDIX 4

IDENTITY AND NUMBER OF PREY OF THE *Bufo marinus* FROM THE SAMPLES COLLECTED AT DARU, TALASEA, AND WARIARATA

MOLLUSCA

Gastropoda—34 small forest snails

ARTHROPODA

Chilopoda—3 centipedes

Diploda—24 millipedes

Arachnida
  Araneae—2 spiders
  Scorpiones
    Scorpionidae—1 scorpion

Insecta
  Isoptera—10 termites

  Mantodea
    Mantidae—1 praying mantis

  Orthoptera
    Gryllidae—11 *Acheta commoda* and 2 *Brachytrypes achatinus*
    Gryllotalpidae—2 *Gryllotalpa africana*

  Hemiptera
    Cicadidae—9 emerging cicada nymphs
    Coreidae—4 plant bugs

Pentatomidae—3 shield bugs
Cydnidae—9 *Adrisa* sp.
Gelastocoridae—2 *Nerthra* sp.

Coleoptera
Haliphidae—3 small water beetles
Curculionidae—11 weevils including 4 *Meroleptus squalidus*, 2 *Rhinoscapha* sp., 2 *Elytrochielus graniger*, and 2 *Cryptorhinus* sp.
Elateridae—6 *Lacon* sp.
Tenebrionidae—169 including 166 *Tribolium* sp. from Daru
Lagriidae—1
Helodidae—187 from Talasea
Cerambycidae—13 unidentifiable longhorns
Chrysomelidae—1 leaf beetle
Byrrhidae—2 pill beetles
Chelonariidae—2
Scarabaeidae—20 including 6 *Lepidiota* sp., 2 *Aromala* sp., and 9 Hybosorinae
Copridae—2 dung beetles
Lucanidae—1 stag beetle and 4 unidentifiable beetles

Diptera—5 unidentified pupa
Statiomyidae—1 horsefly larva

Trichoptera—2 caddis flies

Lepidoptera—9 unidentified larvae
Geometridae—1 geometrid larva

Hymenoptera
Vespidae—2 wasps
Formicidae—190 ants including 133 *Oecophylla smaragdina*, 26 *Pheidole megacephala*, and 31 *Polyrachis*

CHORDATA

Amphibia
Bufonidae—2 *Bufo marinus* juveniles

NOTE: Samples collected at Daru and Wariarata during April 1972; samples collected at Talasea during May 1972. Sample sizes are: Daru, 90; Talasea, 31; and Wariarata, 17.

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